GROOMING BEHAVIOR IN COLEOPTERA

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Abstract

Grooming movements in Coleoptera are divided into 3 categories: 1) cleaning: appendages are passed through the mouth; 2) rubbing: with one or more legs; and 3) positioning: involving adjustment of the elytra, wings, or abdomen. Cleaning movements involve placing an antenna, palpus, fore-, mid-, or hindleg in the mouth, either with or without the assistance of another leg. Rubbing involves all possible combinations of a leg with another appendage or body surface and includes both unilateral and bilateral movements. Positioning includes elytral raising, wing extension and retraction, wing unfolding and refolding, and various body movements. Twenty-one basic grooming acts and over 50 modifications are described. The literature is reviewed and there is a discussion of variation and its possible sources. Data are from the following 38 families: Alleculidae, Anobiidae, Anthicidae, Anthribidae, Apionidae, Attelabidae, Bostrichidae, Bruchidae, Buprestidae, Cantharidae, Carabidae, Cerambycidae, Chrysomelidae, Cicindelidae, Cleridae, Coccinellidae, Cucujidae, Curculionidae, Dermestidae, Elateridae, Histeridae, Lampyridae, Languriidae, Meloidae, Melyridae, Mordellidae, Nemonychidae, Nitidulidae, Oedemeridae, Ptilodactylidae, Pyrochroidae, Rhynchitidae, Scaphidiidae, Scarabaeidae, Scolytidae, Silphidae, Staphylinidae, and Tenebrionidae.

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Introduction

Grooming involves " . . . complex movements which are among the most stereotyped in all the . . . repertory." That comment about ants, by E. O. Wilson (1962), is generally applicable to Coleoptera. Beetles with missing or abnormal appendages attempt identical acts as normal individuals, even though the actual grooming is impossible. For example, the stump of a foreleg

will rotate, the head will turn, the antennae will lay back, and the mouthparts will work to clean a fore tibia and tarsus accidentally lost. Wilson goes on to say that " . . . notes on a wide range of genera confirm that self-grooming behavior varies widely within the Formicidae and thus offers excellent new characters for evolutionary studies. It can be further noted that it is not the basic movements themselves that vary greatly, but rather the pattern of their presence or absence (p. 411)." In comparison, my notes on 33 families of Nearctic Coleoptera indicate that: 1) the grooming repertory of some is richer than that of ants; 2) there is considerable variation in basic movements, both within and between species; 3) the presence or absence of an item in the repertory may vary within individuals of the same species; 4) grooming offers excellent new characters for behavioral and evolutionary studies.

Before I describe the basic repertory of Coleoptera, a few miscellaneous problems require clarification or comment. I use the word "grooming" to describe the broad spectrum of activities under discussion; this includes several cleaning movements, but in other instances, the insect appears no cleaner after the act. The word "preening" was also considered, but in birds this can involve the transfer of oils to the areas involved; in beetles the passing of appendages through the mouth may be partly analogous, but rubbing the body with a leg or adjusting the wing position does not seem to be comparable. Grooming acts are performed at varying intensities; e.g., in the weevil genus *Conotrachelus,* the ipsilateral mid- and hindleg can be raised and rubbed slowly together with the tarsi clear of the substrate and the body stationary, or the act can be performed more rapidly with the tarsi alternately hitting the substrate and the body bumping up and down.

Grooming behavior can be classified in a variety of ways. It is important to distinguish between oral and pedal grooming. I restrict the word "clean" to situations where appendages are passed through the mouth, and I use the word "rub" for a variety of actions involving moving or progressive contact of a leg with another appendage or the general body surface. Not all grooming is included in these categories (e.g., the stereotyped unfolding and refolding of wings). A classification can also consider unilateral vs. bilateral movements, or simple (1 moving part) vs. complex (2 or more moving parts). In practice, all of these categories are useful. Basically, beetles clean legs, antennae, or palpi, with the mouthparts, they rub parts of the body or the antenna with one or more legs, they rub various legs together both unilaterally and bilaterally, and they reposition the elytra, wings, and other body parts. In some species, the sequence of rubbing acts results in the anterior movement of detritus to the mouth.

My observations utilized individuals of unknown age and history, brought into the laboratory, placed in 4 to 8 dram vials, and usually studied under a binocular microscope. Larger beetles were observed in containers commensurate with the size and agility of the insect. For most, a small plastic refrigerator crisper about 10 × 15 × 10 cm, lined with a damp paper towel, worked well. An effort was made to supply food, water, and traction. When possible, only healthy, active specimens were used. The material examined ranges from many dozens (some Anthribidae and cultured species) to only single specimens of a few families.

Many of the species studied are still incompletely determined, and additional material is added daily. I have limited this discussion to the family level, and reserved the details of species, localities, inter-, and intrafamilial variation

for subsequent studies. Most of the taxa are common spring or early summer species in Ohio, others are common stored product pests, and lesser numbers have been collected in the Bahama Islands, Tennessee, Florida, Oklahoma, and Arizona. Almost all specimens are set aside in my personal collection, all are available for study by specialists, and all are labeled as having participated in these studies. I made or verified all observations.

Grooming Movements of Coleoptera

Cleaning

(Appendages passed through the mouth; almost always unilateral)

1) *Antenna Clean.* Usually the fore tibia or tarsus reaches forward and upward over the ipsilateral antenna and pulls it down into the mouth where it is manipulated with a chewing motion. The mouthparts progress from near the antennal base to the apex, as the terminal segment is completed, the antenna springs free. The precision with which this movement is completed appears to vary widely. Some individuals position the antenna in the mouth almost every time, others of the same species need many attempts. Some species perform *Antenna Clean* with relatively high frequency, others seldom or never. Some beetles appear to combine *Head Rub* and the start of *Antenna Clean* in one continuous movement, in others the 2 are clearly separable; these 2 extremes grade into each other so that some observations cannot be allocated with certainty. In 1*a*: held, the customary method, the fore tibia or tarsus remains positioned transversely across the tips of the mouth parts and helps hold the antenna in place in the mouth; a curious variant mode occurs in Cleridae and Melyridae where the 2 forelegs can be crossed under the mouth to hold an antenna in place; in 1*b*: free, the foreleg is positioned in midair or returned to the substrate after pulling the antenna to the mouth, and the maxillae or mandibles hold the antenna in place; in 1*c*: unassisted, the foreleg is not involved, the antenna deflecting into the mouth due to its own musculature; this has been observed only in the family Cantharidae; in 1*d*: double, both antennae are passed simultaneously through the mouth with the aid of one foreleg, observed in Melyridae; and in 1*e*: contralateral, the antenna is pulled down into the mouth by the fore tarsus of the opposite side, observed only in the weevil family Rhynchitidae. *Antenna Clean* has been observed in 27 families of Coleoptera; it appears to be absent in most weevils, Carabidae, Cicindelidae, and some Cerambycidae and Meloidae.

2) *Foreleg Clean.* Usually the apical portion of a fore tibia and all of the fore tarsus is drawn through the mouthparts, however, some beetles include the femur. There is a continuum between deliberate passage of the foreleg with associated chewing motions, to very rapid passage without observable mouth movements—the leg appearing to slide rapidly through the mouthparts without being manipulated. During rapid passes, leg movement through the mouth can be unidirectional or back and forth, while in the slow "chewing" passes, the mouthparts progress apically to the tarsal claws. Three clearly different modes were observed (2 may be abnormal). They are 2*a*: ventral, the customary method where the leg is raised beneath the head, the tarsus

projects anteriorly, and the leg is drawn posteriorly; 2*b*: reverse, where the foreleg is raised in front of the face, the tarsus projects downward and posteriorly into the mouth, and is drawn anteriorly through the jaws, observed twice in one specimen of an undescribed species of Anthribidae; and 2*c*: bilateral, where both tarsi are drawn posteriorly through the mouth simultaneously, observed only in some Staphylinidae. *Foreleg Clean* has been observed or reported in 29 families, and appears absent in non-anthribid weevils and Cicindelidae.

3) *Midleg Clean.* The tarsus or tibia and tarsus of the midleg is drawn through the mouth usually with definite chewing motions, the claws last. There are 5 clear-cut modes. 3*a*: ventral, the midleg is brought forward beneath the body and the mouth dips downward and backward to reach it; observed in Anthribidae; 3*b*: lateral under, the midleg is turned forward alongside the body, the head turns to that side, and dips laterally and backward to reach it; in this mode the midleg crosses under the ipsilateral foreleg which can be raised or else remains on the substrate, observed in 5 families, Anthribidae, Anthicidae, Cantharidae, Cleridae, and Coccinellidae; 3*c*: lateral over, similar to the previous mode except the midleg crosses over the ipsilateral foreleg, observed in certain Anthribidae, Bruchidae, Cerambycidae, and Melyridae; 3*d*: lateral pull, where the foreleg hooks over the ipsilateral mid tibia and draws it forward so that the mouth reaches the mid tarsus, reminiscent of a praying mantis; observed only in 1 anthribid weevil; 3*e*: lateral push, where the midleg is moved forward and placed across and over the apex of the fore femur which is raised and used to push the mid tarsus to the mouth, this is one step beyond the lateral over mode (#3*c*), for the foreleg is raised from the substrate; has been observed in some Bruchidae and Cerambycidae. In addition to these 5 modes, anthribids and clerids have been observed with fore and mid tarsi of one side in the mouth simultaneously. This may be a distinct grooming act (*Fore-Midleg Clean*), but since the start of the act was not seen, it is presently considered an abnormal *Midleg Clean* where the foreleg got involved. *Midleg Clean* has also been reported in Meloidae and Oedemeridae (Jander, 1966).

4) *Hindleg Clean.* The hind tarsus is drawn through the mouth with definite chewing motions, the claws last. Three clear-cut modes occur, and the possibility of others exists. 4*a*: ventral, where the hindleg is brought forward beneath the body, and the head stretches downward and backward so that the mouth reaches the hind tarsus; this can be assisted or not by the mid tarsus; known only in Anthribidae; 4*b*: fore pull, can be achieved in 2 ways, where the hindleg is rotated forward lateral to the body and the foreleg is hooked over it and draws it forward so that the mouth reaches the hind tarsus, in Anthribidae and Anthicidae, and where the hindleg is raised vertically, then continues forward until the foreleg hooks over it and pulls it down to the mouth; known only in Anthicidae; the latter variant can end with the hindleg either over or under the midleg, both being observed in the same individual. 4*c*: mid pull, same as the first variant of 4*b*, except the midleg pulls the hind to the mouth, known only in Anthribidae.

5) *Palpus Clean.* The palpi of one side are curled into the mouth and chewed by the maxillae, with the mandibles or fore tarsus helping to maintain the position, observed several times in Anthicidae, Cantharidae, Cleridae, and Ptilodactylidae.

RUBBING
(With one or more legs; unilateral unless stated otherwise)

6) *Antenna Rub.* Portions of a fore tarsus or tibia are rubbed along the dorsal surface of the ipsilateral antenna, starting at or near the base and progressing distally. This action can be performed while standing or walking (even rapidly), and in several very distinct modes; 6*a*: substrate, where the antenna is stepped on by the ipsilateral foreleg (by the midleg in a few Anthribidae and Chrysomelidae), pressed against the substrate, and pulled clear; 6*b*: aerial, where the foreleg rubs along the antenna in mid-air anterior or lateral to the head and the antenna remains clear of the substrate; 6*c*: bilateral, where each antenna is rubbed by its ipsilateral foreleg simultaneously, can be in either substrate or aerial modes, has been observed in 8 widely different families; 6*d*: contralateral, where the head is turned to one side and the more ventral antenna is rubbed by the foreleg of the opposite side, has been seen in Curculionidae; 6*e*: bipedal, where the antenna is pulled or rubbed between the appressed ipsilateral fore- and midlegs, this occurs in some Cerambycidae and Chrysomelidae, and explains the function of the grooves on the fore and mid tibiae of the cerambycid subfamily Lamiinae; 6*f*: retracted, where the antenna is withdrawn under the head and rubbed with the dorsal surface of the foreleg in an anterior to posterior "come-hither" motion, observed in Bostrichidae and Scarabaeidae; 6*g*: ventral, where the foreleg contact is on the underside of the antenna, observed once in Anthribidae; 6*h*: double, where both antennae are rubbed simultaneously by one foreleg, also observed once in Anthribidae. *Antenna Rub* has been observed in 29 families; the many modes (and the subtle variations not detailed here) indicate the need for much additional study.

7) *Head Rub.* Portions of a fore tarsus or tibia are passed over any part of the head. Usually there is an accompanying coordinated head movement which facilitates reaching the area to be rubbed. In Anthicidae, Anthribidae, Bostrichidae, Bruchidae, Cerambycidae, Cleridae, Coccinellidae, Elateridae, and Lampyridae, the *Head Rub* can originate on the prothorax, but in most beetles it is restricted to the head; 7*a*: unilateral, is the customary act; 7*b*: bilateral, where both forelegs are used simultaneously or alternately; occurs in scattered families. When alternate, the choice between unilateral and bilateral modes can be arbitrary, I have based it on the speed, degree of continuity, and the extent to which both forelegs are off the substrate at the same time. Although *Head Rub* has been observed in 31 families, it clearly is not as variable as *Antenna Rub.* One probable source of variation which has not been investigated is the position of antennae during the act.

8) *Body-Midleg Rub.* Portions of a mid tibia or tarsus are rubbed over the surfaces of the head (rarely), pterothorax, or abdomen; 8*a*: unilateral, is the customary mode, observed in 23 families; 8*b*: bilateral, is infrequent in beetles, having been observed in Cantharidae, Cerambycidae, Cicindelidae, Cleridae, Curculionidae, and Lampyridae. The most extensive movement was seen in some Anthicidae and Curculionidae, where the midleg was able to rub the entire dorsal surface from the eyes to the pygidium.

9) *Body-Hindleg Rub.* As in number 8, but the hindleg is used. Present in most beetles studied adequately (30 families) and may be universal in the Coleoptera. The leg motion can be in anterior-posterior sequence or, more rarely, back and forth. In addition to the major modes, 9*a*: unilateral; and 9*b*:

bilateral; there appear to be important differences in the parts of the body contacted. These include the usual dorsal, lateral, and ventral surfaces, and also 2 rare modifications: alar, where the elytron is raised and the hind tarsus rubs the dorsum of the wing; seen in some Anthicidae, Attelabidae, Bruchidae, Cerambycidae, Cleridae, and Melyridae; and tergal, where the elytron and wing are both raised and the hind tarsus rubs the abdominal tergites (or perhaps the wing venter?) as in Anthicidae, Attelabidae, Bruchidae, Cantharidae, Cleridae, Melyridae, and Staphylinidae. A possible third mode, rudimentary, (perhaps abnormal) was observed in the weevil genus *Lechriops*, where the femur swings anteriorly and posteriorly, the tibia kicks, and the tarsus twitches, but the leg does not contact the body. In some Bruchidae the act can involve the dorsum of the head.

10) *Body-Mid-Hindleg Rub.* Essentially a combination of numbers 8 and 9, where mid- and hindleg of one side are simultaneously rubbed over the dorsum of the body. In 10*a*: sequential, the hindleg remains posterior to the midleg; in 10*b*: reversed, the 2 legs are crossed, the hind tarsus being anterior to the mid tarsus during the act. Of the 14 families with this type of grooming, only the Bruchidae utilized the reversed mode; 2 (Anthribidae and Cantharidae) have a rare bilateral variant, and 1 (Melyridae) has alar and tergal options as outlined in #9 above.

11) *Body-Mid-Mid-Hindleg Rub.* This 3-legged movement has been observed only in Cerambycidae and Melyridae.

12) *Body-Mid-Hind-Hindleg Rub.* This is the other 3-legged body rub; it occurs in some Cerambycidae and Chrysomelidae.

13) *Bilateral Foreleg Rub.* The 2 forelegs are entwined or rubbed together. There are 2 basic positions, 13*a*: anterior, where the legs reach around the head and the rubbing is anterior to it; 13*b*: posterior, where rubbing takes place beneath the head, posterior to the mouthparts. The former mode occurs in Attelabidae (Daanje, 1964) and various Curculionidae, the latter in some other Curculionidae as well as Cerambycidae and Melyridae. The act has also been observed in Cleridae, but the mode was not recorded.

14) *Fore-Midleg Rub.* Fore and mid tarsi or tibiae and tarsi of one side are entwined or rubbed together. This movement varies greatly in frequency and may be absent in some individuals or species. There are 2 modes for this movement but they can be combined in some species; 14*a*: substrate, where 1 leg, usually the middle, does not leave the substrate and is rubbed by the other; 14*b*: raised, where both legs are lifted and rubbed together. In some beetles both tibia and tarsus are involved; in others, only the tarsus. This common movement has been seen or reported in 30 families of Coleoptera.

15) *Mid-Hindleg Rub.* Mid and hind tarsi or tibiae and tarsi of 1 side are entwined or rubbed together. The modes 15*a*: substrate, and 15*b*: raised, are as in 14 above and can run together or alternate in a single bout of grooming; however there is a third mode 15*c*: bilateral, which involves simultaneous rubbing together of all 4 mid- and hindlegs beneath the abdomen. The customary substrate or raised modes occur in 30 families of beetles, while the rare bilateral mode has been seen in Anthribidae, Cantharidae, Cerambycidae, Chrysomelidae, Curculionidae, and Nemonychidae.

16) *Bilateral Hindleg Rub.* The 2 hindlegs are rubbed together beneath the abdomen. Observed in 18 beetle families.

17) *Fore-Mid-Hindleg Rub.* In this curious action, the 3 legs of 1 side are brought together and rubbed simultaneously. Observed in Anthicidae,

Bruchidae, and Staphylinidae. In the last family the body is tilted and curved, supported by a tripod of 3 legs, and the rubbing motion is raised, not substrate. In some Anthicidae the midleg is never or seldom used; this can result in a *Fore-Hindleg Rub.*

Positioning
(Unilateral or bilateral)

18) *Elytra Raise.* A rapid rise and fall of the elytra usually with slight separation. This is the most widespread positioning movement, but detailed records for this and the following actions are incomplete.

19) *Wing Extend.* The wing apex is straightened and extended to its full length beyond the abdomen, and then retracted more slowly. In this action the wing remains folded longitudinally and is not ready for flight. This movement can be preceded by *Elytra Raise* (#18), and is sometimes accompanied by various modes of *Body-Hindleg Rub* (#9). The extension can be sudden or laborious and can be assisted or not by abdominal pulsations; the retraction is usually gradual and may or may not be assisted by the abdomen. For example, in some Bruchidae the abdomen functions in wing retraction but not extension, and in Curculionidae the abdomen functions in both. During abdominal assistance, the elytra are usually closed.

20) *Wing Unfold.* The elytra and wings are raised and spread, and the wings are completely unfolded, as if for flight; then refolded. The refolding can involve abdominal assistance.

21) *Vessicle Extend.* Membranous intersegmental vessicles are inflated by body contraction and then withdrawn into the body out of sight. This is done during a bout of grooming interspersed with various other movements, and does not appear correlated with response to external stimuli. Observed in an unidentified melyrid which has a large curved Y-shaped yellowish-gray vessicle on each side in the membrane between the metacoxa and the abdomen. The insect groomed various external parts, then braced itself, curled and contracted the abdomen to the side, extended and retracted 1 vessicle in a smooth continuous motion, resumed other grooming, and then repeated the procedure on the other side.

Discussion

A number of factors clearly affect the overall picture of grooming activity; there are probably many others. The most important of these is the fact that the complete grooming repertory is not always seen in 1 individual, even after hours of observation. This can be due in part to varying grooming intensity, for it is clear that some beetles have 2 different repertories which are involved at different times. There can be a frequently observed routine involving mostly *Body* and *Leg Rubs,* and a special repertory, observed infrequently, involving oral cleaning and some rubbing acts. Since the stimuli which initiate each type of grooming activity have been incompletely checked (by experimental application of dusts, water, irritant liquids, pressure, etc.), it sometimes requires long observation to obtain a reasonably complete picture. It is also clear that the state of activity affects grooming, (e.g., some beetles appear to groom at almost any time, while others do little or no grooming

when disturbed and have a more complete repertory shortly before settling down and becoming immobile). The nature of the substrate has an effect involving traction and probably chemoreception; some beetles have an incomplete repertory in an empty vial, and a more diverse one when they can stand on a piece of bark or dead leaf. The availability of food and water seems to stimulate either the frequency or diversity of grooming in at least some cases and undoubtedly is involved also in the substrate reaction. Inadequate atmospheric humidity, varying temperature, light intensity, past contact with insecticides, age, and nutritional history all introduce variables which affect the grooming repertory. Finally, in some vertebrates, grooming is a common form of displacement activity; it is not clear to me if this applies to grooming in Coleoptera.

Knowledge of grooming behavior in the Coleoptera is still in its infancy. It was hoped that the literature might fill some of the gaps, but very few papers mention beetle grooming behavior. In Attelabidae, Daanje (1964), discussing *Deporaus betulae* (L.), mentions what I have called *Antenna Clean, Head Rub, Antenna Rub, Body-Midleg Rub, Body-Hindleg Rub, Fore-Midleg Rub, Mid-Hindleg Rub,* and *Hind-Hindleg Rub*; and for *Apoderus* he mentions a *Fore-Foreleg Rub.* In Bruchidae, Forister and Johnson (1971) mention a male *Acanthoscelides prosopoides* which, during copulation, groomed " . . . his legs and antennae with his fore legs . . . with his hind legs balancing him." I interpret this as *Antenna Rub* and *Fore-Midleg Rub,* which coincides with my observations of the same genus. In Carabidae, Hlavac (1972) presents a fine discussion of the fore tibial antenna scraper, and for *Scaphinotus* and *Pristonychus* describes *Foreleg Clean, Antenna Rub,* and *Fore-Midleg Rub.* In Cerambycidae, Chemsak and Linsley (1971) observed in *Rosalia funebris* what appears to be an incomplete bilateral *Antenna Rub* involving only the scapes; Chemsak and Powell (1971) mentioned that *Leptalia macilenta* utilizes *Antenna Clean, Foreleg Clean,* and *Fore-Midleg Rub*; and B. D. Blair (pers. comm.) has seen *Antenna Rub* in *Dectes.* In Elateridae, Lilly (1959) mentions *Antenna Rub* in *Limonius californicus* in response to very dilute hydrochloric acid. My data for several species each of Carabidae, Cerambycidae, and Elateridae verify and extend these reports. In Meloidae, Selander (1964) states that *Pyrota nigrovittata* grooms the fore legs (? with the mouth) and the body with the hind legs; Selander and Pinto (1967) point out that in *Meloe, Lytta,* some *Linsleya,* and *Pyrota* the antennae are cleaned with the mouth, while in *Epicauta,* some *Linsleya* and *Pleuropompha* the antennae are groomed with a special groove on the fore leg; Selander and Mathieu (1969) mention what I call *Foreleg Clean, Midleg Clean, Antenna Rub, Head Rub, Body-Midleg Rub, Body-Hindleg Rub,* and *Mid-Hindleg Rub* in *Epicauta*; the two *Body-Leg Rubs* also include rubbing the metathoracic wings.

In the most important paper on grooming in Coleoptera, Ursula Jander (1966) has provided an overview of the tracheate arthropods, including 14 families and 31 species of beetles. Among these, the broadest coverage is of Cerambycidae (6 species) and Carabidae and Silphidae (4 species each). Only 1 representative of Chrysomelidae was studied and 3 of Curculionidae (*sensu lato*). Jander's work utilizes only 8 grooming movements: *Antenna Clean* (my #1), *Foreleg Clean* (#2), *Midleg Clean* (#3), *Antenna Rub* (#6) in both unilateral and bilateral modes, *Fore-Midleg Rub* (#14), *Mid-Hindleg Rub* (#15), *Hind-Hindleg Rub* (#16). None are universal within the order. In the English summary she states (p. 842) that (with few exceptions) myriapods,

thysanurans, and orthopterans (*sensu lato*) " . . . groom the antennae and all of the legs with the mouthparts. This method is therefore to be regarded as the primordial mode of grooming in the Tracheata . . . No grooming of the hindlegs with the mouthparts was observed among beetles. However, Cantharidae and Oedemeridae are still able to groom the antennae and the first two pairs of legs with the mouthparts. In other beetle groups, these primordial grooming actions are partially or entirely replaced (by rubbing with the legs)." Because hindleg cleaning (with the mouth) was not observed in beetles, Jander isolates the order in a grooming level (her Fig. 21) between the primitive myriapod-thysanuran-orthopteran pattern (mouth usually cleans all appendages) and the remaining Insecta (antennae and then 2 or 3 pairs of legs cleaned by the legs, not by the mouth). The families Anthribidae and Anthicidae destroy this distinction and broaden the diversity of the Coleoptera to overlap the grooming level of the primitive tracheates. Jander's diagram does not show the variation of the various orders, but only the maximum degree of oral grooming present in the group. Jander's concept that oral grooming is primitive is probably true among tracheates generally, but in Coleoptera mid- and hindleg cleaning is associated primarily with species which contact pollen, spores, or other finely particulate substrates.

Among the better studied families of Coleoptera, the most diverse patterns presently are found in the families Anthicidae, Anthribidae, Bruchidae, Cerambycidae, Chrysomelidae, Cleridae, Coccinellidae, Melyridae, and Staphylinidae. Looking at grooming diversity in the order, it is clear that some movements will provide much more information for studies of comparative behavior and evolution than others. The most obvious are the cleaning movements (oral grooming) and the more unusual types of rubbing movements (pedal grooming). The known distribution of these acts has been outlined above; their interest and importance in future studies is self-evident.

Although no grooming movement occurs throughout the order, most of the beetle species studied to date have a basic pattern of 5 similar grooming movements (#6, 7, 9, 14, 15). Studies of these basic acts should include: verification of their presence or absence in additional taxa, search for distinctive modes and postures during these movements, and recording the sequence of grooming actions to provide clues to the evolution of this behavior, and suggest functional or genetic similarities between taxa.

Every family studied grooms the antennae, either by *Antenna Clean* or *Antenna Rub,* and most do both. Every family studied (except the Scarabaeidae) grooms the forelegs by either *Foreleg Clean* or *Fore-Midleg Rub,* or both. Scarabs probably do it too, but data on them is fragmentary. Reduction of oral grooming is strongly correlated with either special rubbing structures or techniques. The corbels and other spiny tibial fringes of weevils are literally used as combs to rake the ventral tarsal surfaces, and the protibial scrapers of Carabidae, the protibial groove of some Meloidae, and the mesotibial groove and protibial sinus of lamiine Cerambycidae are all used for antennal grooming, and occur in species where *Antenna Clean* has not been reported. The absence of special structures can be balanced by special techniques. In weevils, where one of the principal evolutionary trends has been the reduction and consolidation of the mouthparts, *Antenna Clean* is absent in the vast majority of species, however *Antenna-Foreleg Rub* is performed in 4 different modes (substrate, aerial, bilateral, and contralateral), and some species utilize 3 of the 4 possibilities.

The correlation of grooming behavior with current ideas of beetle classification is still difficult to predict, for the similarities and differences between taxa may be artifacts of the sample. Fourteen beetle superfamilies are represented, but by relatively few species. It is clear that many families are different; for example, all 9 genera of Tenebrionidae examined include 8 major grooming movements, while 2 species of Anthicidae include 16 major movements and many variations, and 3 genera of Scarabaeidae include only 4 movements (all in 1 specimen). The quantity (and quality) of these differences correlates best with activity and habits, not phylogeny, and I suspect this is the principal pattern. At present, the only clearcut relationship between grooming behavior and phylogeny is the rapid reduction and loss of oral grooming in the derivative Rhynchophora, and the concomitant development of special rubbing structures and movements. The loss of oral antennal cleaning in Adephaga, at the opposite end of the order, clearly indicates that this type of behavior (and others) can arise independently within the order.

Summary

1) Data on grooming are presented for 38 families of Coleoptera: Alleculidae, Anobiidae, Anthicidae, Anthribidae, Apionidae, Attelabidae, Bostrichidae, Bruchidae, Buprestidae, Cantharidae, Carabidae, Cerambycidae, Chrysomelidae, Cicindelidae, Cleridae, Coccinellidae, Cucujidae, Curculionidae, Dermestidae, Elateridae, Histeridae, Lampyridae, Languriidae, Meloidae, Melyridae, Mordellidae, Nemonychidae, Nitidulidae, Oedemeridae, Ptilodactylidae, Pryochroidae, Rhynchitidae, Scaphidiidae, Scarabaeidae, Scolytidae, Silphidae, Staphylinidae, and Tenebrionidae. Ninety-eight genera in 33 families have been observed by me, and an additional 33 genera and 5 families are briefly or incompletely mentioned in the literature.

2) Grooming behavior varies in both the presence and performance of an item in the repertory, and can be affected by the individual's state of activity, substrate, availability of food and water, temperature, light, humidity, exposure to insecticides, age, and nutritional history.

3) Distinction should be made between oral grooming (cleaning) and nonoral grooming (rubbing and positioning), between uni- and bilateral movements, and between 1 moving part (simple) and 2 or more coordinated moving parts (complex).

4) The most widespread grooming movements in Coleoptera are *Antenna Clean, Foreleg Clean, Antenna Rub, Head Rub, Body-Hindleg Rub, Fore-Midleg Rub,* and *Mid-Hindleg Rub.* The last 5 (the rubbing movements) have been seen in most beetles, but at present no movement is universal in Coleoptera.

5) Several species of Anthribidae and Anthicidae are the only known beetles which can clean the hind tarsi with the mouth. In fact, Anthribidae have 4 ways of doing this, and Anthicidae have 2. According to Jander (1966), this is "primordial" among tracheate arthropods.

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Book Review

Readings in Entomology by Pedro Barbosa and T. Michael Peters. 1972. W. B. Saunders Co., West Washington Square, Philadelphia, Pa. 19105. 450 p.; 303 Fig. (7 1/4" × 10 1/4"). Paperbound, $6.50.

As the title indicates, this is a collection of articles which previously appeared in scientific journals. Although designed primarily to up-date and supplement college texts, it is worthwhile reading for those entomologists who graduated some time ago. The most difficult task for the authors was to make the selections from such a mountain of relative literature. The "Annual Reviews" try to cover the same thing except by review articles in a particular subject.

The idea of reproducing published papers in such a collection presents an inexpensive printing method. No composition costs are involved because camera ready copy is used. The illustrations suffered in some cases, but otherwise the result is adequate.—R. E. Woodruff